THE MICROSTRUCTURE AND MINERALOGY OF THE SHELL OF A JURASSIC MYTILID (BIVALVIA)

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ABSTRACT. Well-preserved shells of *Praemytilus strathairdensis* (Anderson and Cox) from the Great Estuarine Series (Middle Jurassic) of the Isle of Eigg, Scotland, are described with special reference to their microstructure, mineralogy, and chemical composition. Both the main calcareous shell layers are nacreous, with the crystal structure apparently identical to modern nacre. Myostracal layers are composed of prismatic aragonite; calcified traces of the periostracum have been observed. The inner layer shows sub-layers defined by variations in thickness of the nacreous laminae. These probably represent seasonal growth. Mineralogically, the shells are wholly aragonite, with a high strontium content compared to modern bivalves. The organic matrix is in part physically preserved but with altered ultrastructure; it is reduced in amount from the probable original value and the carbon–nitrogen ratio is much higher. The species is one of the earliest representatives of *Mytilus sensu lato*; the structural data agree with this. The aragonitic composition suggests warm temperatures, by comparison with modern Mytilidae; the growth pattern suggests the existence of seasons.

IN 1930 Bøggild laid the foundations for all subsequent studies of molluscan shell structure in a classic paper in which he defined the different types of structure and surveyed their distribution, and that of aragonite and calcite mineralogies, among the Mollusca. He was extremely cautious in offering interpretations of his extensive observations, but clearly showed that shell structure is of potential importance in taxonomy. The taxonomy he himself used is not entirely satisfactory and there is no doubt that some of his material, from old museum collections, was misleadingly identified (Schenck 1934, Lowenstam personal communication). Newell (1937, 1942, 1965) is one of the few authors who has critically studied shell structure in connexion with systematic palaeontology.

In recent years it has become clear that shell structure is in part ecologically, as well as taxonomically, controlled; high temperatures have been shown to favour aragonite over calcite in the molluscan shell (as well as in other phyla), so that warm-water and cold-water species of the same genus, or other taxon, differ in their mineralogy (Lowenstam 1954*a*). This mineralogical change necessarily involves also a change in shell structure, as in *Chama* (Lowenstam 1954*a*, 1963). Striking instances of this effect occur in the Mytilidae. Lowenstam (1954*a*) found that the tropical species he examined were 100% aragonite, whereas the temperate species, particularly *Mytilus californianus*, were composed of aragonite plus calcite with the aragonite percentage positively correlated with temperature. The results on the temperate species have recently been extended by Dodd (1963, 1964, 1965) who considered shell structure and trace-element concentrations as well as mineralogy, and by Hare (1963) who has studied the composition of the the organic matrix. Some tropical species have been examined in detail by Hare, Hudson, and Lowenstam (unpublished data).

The existence of this unusually good, though still incomplete, knowledge of the modern forms, together with the apparent coherence of the Mytilidae over long periods of geological time, makes investigations of fossil representatives of this family an attractive proposition. This paper is a description of some unusually well-preserved shells of the

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Jurassic species *Praemytilus strathairdensis* (Anderson and Cox) with a brief discussion of the taxonomic and ecological implications.

OCCURRENCE AND PRESERVATION

Mytilus (*Praemytilus*) *strathairdensis* was described by Anderson and Cox (1948) from the Great Estuarine Series (Middle Jurassic) of Strathaird, Isle of Skye, Scotland. Their material consisted of internal and external moulds in hard shale. The species also occurs, with the shell well preserved, in the Isle of Eigg, 18 miles south of the Skye locality. Both localities are in the Mytilus Shales of the Great Estuarine Series; the species is known only from this formation and has not been found outside the Hebrides. All the material for the present study came from Bed 5 of the type locality of the Mytilus Shales in Eigg (Hudson 1963, p. 338; pl. 53, fig. 6). A detailed account of the stratigraphy and palaeoecology of the Mytilus Shales is given by Hudson (1966).

The material consists of shells preserved in shell-layers in soft silty shales; most are disarticulated but some have the valves still associated. They are translucent and have a pearly lustre, though without the brilliant iridescence shown by some fossil nacreous shells. They are unfortunately very fragile mechanically. In associated beds the shells are found in various stages of diagenetic alteration. This subject will be treated in more detail elsewhere (Hudson, 1965, abstract).

SHELL MORPHOLOGY

The species *Mytilus* (*Praemytilus*) *strathairdensis* was described by Anderson and Cox (1948) who created the monotypic subgenus *Praemytilus* for it. Their diagnoses were as follows:

Subgeneric characters. Shell much resembling *Mytilus s. str.* in shape, with a rather broad, reflected marginal area, without teeth, in the umbonal angle, and with a deep, elongate anterior adductor scar close and parallel to the antero-ventral margin. Ligament supported by a sub-internal ridge, as in *Mytilus s. str.*

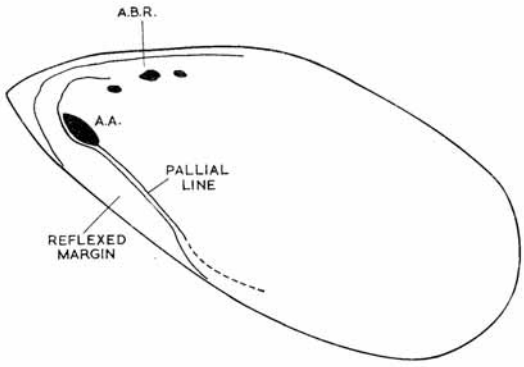
Specific characters. Medium size for a Mytilid, obliquely ovate, of slightly variable proportions; a line from the umbo to the most distant point on the posterior margin usually makes an angle of about 30° with the hinge margin. Umbo terminal. Dorsal margin feebly convex, meeting the moderately convex posterior margin in an even curve; ventral margin evenly convex; anterior lobe undeveloped. Shell evenly inflated except for a slight postero-dorsal flattening; no umbonal ridge. Surface unornamented, but with pronounced, irregular growth rugae. Anterior adductor scar deep and elongate, extending from the umbonal angle in a direction parallel to the antero-ventral margin.

The holotype measures 29·5 mm. in length and 17·5 mm. in height perpendicular to hinge margin. Anderson and Cox comment on the distinctive, for a Jurassic mytilid, evenly convex outline, and remark that the shell seems to have been very thick.

My material agrees with this diagnosis except that the growth rugae would not be described as 'pronounced' by comparison with most modern Mytilidae, and they are fairly regular in shape, although there are variations in the strength of individual rugae. The shell is thick in the umbonal region, but very thin elsewhere. At the level of taxonomic discrimination used by Soot-Ryen (1955) for recent Mytilidae there is little doubt that *Praemytilus* ranks as a full genus.

The new material enables some details to be added to the description of the internal structure of the shell. The structures are typically mytilid and, as is usual in the family, the details are somewhat variable.

Musculature. The deeply impressed and elongate anterior adductor scar was noted by Anderson and Cox (1948, p. 106). My specimens also show the anterior byssal retractor scar, in a similar dorsal position to that in modern Mytilidae (text-fig. 1, cf. Newell 1942, Soot-Ryen 1955). Both these muscle scars are striated in well-preserved specimens. Sometimes there is another scar below and anterior to the byssal retractor; possibly the termination of this muscle was bifid as shown by Newell (1942) for some Palaeozoic forms. Thus there is direct evidence that the species was byssiferous throughout life. There is no direct evidence of the emergence of the byssus, but by analogy with modern



TEXT-FIG. 1. Interior of right valve of *Praemytilus strathairdensis*, showing musculature. A.A., anterior adductor; A.B.R, anterior byssal retractor (with two small additional muscle scars). The posterior musculature is unknown. Anterior traced from a photograph; posterior outline reconstructed, based on a more complete specimen. $\times 2\frac{1}{2}$.

Mytilus it probably emerged just posterior to the termination of the thickened antero-ventral margin which is described below. Other small muscle scars are seen in the umbonal cavity on some specimens but they are not constant. Probably they bore mantle-attachment muscles. There is often a line of small discrete pits along the anterior part of the pallial line. The posterior musculature has not been seen on any of the specimens or moulds examined. It must have been very shallowly impressed. The shell in this region is very thin and fragile.

Hinge structure and reflexed margin. The most distinctive internal feature of the species is a broad, reflexed, and thickened margin to the antero-ventral part of the shell. It is especially thick, forming a swelling, immediately behind the deeply impressed anterior adductor muscle scar, where it is bordered internally by the pallial line (text-fig. 1). At one-quarter to one-third of the length of the shell the thickened margin fades gradually into the general margin of the shell. From the anterior adductor scar the reflexed margin continues in a smooth curve inside the umbonal region, so that the species has an internal 'platform' which is lacking in *Mytilus s. str.* or other modern mytilids. Usually this platform is quite smooth, so that the shell is edentulous, but in a few specimens

there are corrugations immediately behind the umbo. Unlike the teeth of *Mytilus s. str.*, these are not continuations of grooves across the external lunule which occurs behind the umbo in this position. Traced beneath the dorsal margin, the 'platform' decreases rather rapidly in thickness and disappears in the region of the anterior byssal retractor muscle scar.

The ligament region is marked by a thin and fragile flange, of lesser external convexity than the rest of the shell, which extends from the umbo along the dorsal margin. This easily breaks off in development. In some specimens it can be seen to bear a thin ridge between the dorsal margin and the 'platform', and this apparently continues dorsally beyond the 'platform'. There is no preserved trace of the ligamental ridge of porous, prismatic aragonite which is present in modern Mytilidae, but the thin ridge referred to could correspond to the nacreous ridge which lies below the porous ligamental ridge in the modern forms. The ligament was 'split' and non-functional in adult shells at the anterior end, in the region of the lunule, as in modern *Mytilus* (Stasek 1963, fig. 4D). This is shown by a specimen which has the valves attached where they were held by the ligament but in which they gape in the region of the lunule.

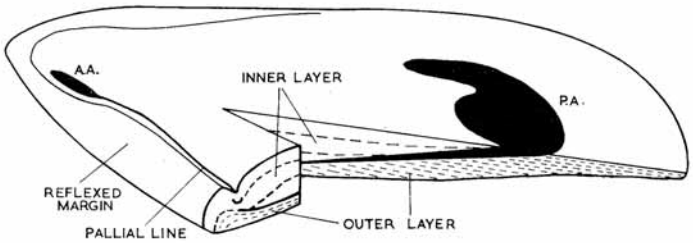
Ontogeny. Juvenile shells are abundant in the rocks studied. Like the juveniles of many other Mytilidae, they are modioliform in shape, with a distinct ventral lobe. The transformation to the mytiliform adults can be followed in the growth-lines of adult individuals. In shells greater than about 5 mm. in length, growth in the plane of the commissure was concentrated in a posterior direction, so that the umbones became effectively terminal. Beneath the umbones growth was almost entirely normal to the commissure in later ontogeny, as the shell inflation increased and the reflexed antero-ventral margin was formed. At a still later stage growth at the shell margin ceased, but the shell was still thickened by the deposition of inner layer material in the umbonal cavity. This is commonly found in modern *Mytilus*.

SHELL STRUCTURE AND MICROSTRUCTURE

The shells of bivalves are composed of structurally and sometimes mineralogically distinct layers secreted by different parts of the mantle, as described in general accounts Yonge (1960), Wilbur (1964), and Mutvei (1964). The outermost layer, the *periostracum*, is secreted by the inner surface of the outer mantle fold. It is not calcified. Inside the periostracum are two or more calcareous layers. In many bivalves two such layers are readily distinguished, an *outer layer* secreted by the outer surface of the outer mantle fold, and an *inner layer* secreted by the whole mantle surface inside the pallial line. Oberling (1964) points out, however, that there are frequently three main calcareous layers, and that these may also be divided into *sub-layers* by alternations of structure within a main layer. He also stresses the importance of structurally distinct layers secreted beneath the muscle attachments. These he terms the *myostracal layers*, differentiated into *adductor myostracum*, etc., according to the muscle concerned. The alternative term 'hypostracum' has been used in conflicting senses for both inner (main) layer and adductor myostracum (Oberling 1955, 1964). The 'Helle Schicht' of Schmidt (1924) refers to adductor myostracum. The classic account of shell microstructure (i.e. the arrangement of crystals and organic matrix within a layer, rather than

the arrangement of layers within a shell) is that by Bøggild (1930) whose terminology will be used here. The individual layers of aragonite crystals in nacreous structure will be referred to as *laminae*.

The shell structure of *Praemytilus strathairdensis* is summarized in text-fig. 2. Apart from rare preserved traces of periostracum, the shell consists of two calcareous layers, a thin outer layer of nacreous structure with fine laminae (less than 0·5 μ) and a thicker inner layer, also nacreous but with coarser (1 μ) laminae; the inner layer is divided into



TEXT-FIG. 2. Reconstruction to show the distribution of shell layers in *Praemytilus strathairdensis*, showing longitudinal and transverse sections. Trend of nacreous laminae schematically shown in outer layer; myostracal layers black; sub-layers schematically shown in inner layer. A.A. anterior adductor; P.A. posterior adductor, conjecturally drawn after modern Mytilidae.

sub-layers. Between the main layers is a thin layer of pallial myostracum. In the hinge region the structure is complex with traces of anterior adductor—and byssal retractor—myostracum preserved.

In thin sections the layers are not always easy to distinguish, but usually the nacreous structure of the inner layer is apparent under high power, and its division into sub-layers is best seen under crossed nicols (Pl. 35, fig. 1). The outer layer appears homogeneous in thin section but its structure is revealed by electron microscopy. Slightly altered shells are often coloured brown in thin section and are pseudopleochroic (Hudson 1962), with Y or $Z > X$, probably due to partial decomposition of the organic matrix. In these shells the outer layer is usually distinctly darker than the inner, and this helps in differentiating the layers.

In the following paragraphs the different shell layers are described in detail, and some special topics are discussed. In view of the importance of nacre in the shell, the microstructure of this material is described first. This paragraph is based mainly on the literature cited, supplemented by personal observations mainly on Mytilidae.

Crystal structure of nacre and its relationship to the organic matrix. The nacreous structure is found in the three main classes of the mollusca but is not known outside that phylum. It is the simplest and also the best-known type of molluscan microstructure. Its distribution within the mollusca is described by Bøggild (1930) and by Oberling (1964), who stress that it is particularly characteristic of the 'primitive' members of the molluscan classes (Archaeogastropods, *Nautilus*, Nuculidae, for instance). The most comprehensive optical study of nacre is by Schmidt (1924); Wada (1961) has published

a very well illustrated account of the crystal structure using electron microscopy and X-ray methods. The organic matrix has been studied, using electron microscopy, by Grégoire, Duchateau, and Florkin (1955) and by Grégoire (1957, 1959, 1962). More details of the relationship between the crystals and the matrix are revealed in an elegant study by Watabe (1965).

Nacre consists of tabular crystals of aragonite arranged in thin parallel sheets (laminae), typically 0·5–1·0 μ thick. These are separated by even thinner sheets of the proteinaceous organic matrix (conchiolin), less than 0·1 μ thick, the *interlamellar matrix*. The individual aragonite crystals within the laminae are separated by *intercrystalline matrix*, and within each single crystal are very fine sheets of *intracrystalline matrix* (Watabe 1965). The pattern formed by the interlamellar and intercrystalline matrices is responsible for the familiar brick-wall appearance of vertical sections of nacre (Pl. 31). The intracrystalline matrix is too fine to be seen with the light microscope and is only imperfectly seen on electron micrographs of surface replicas (like those used here). Its detailed distribution was revealed by Watabe (1965), who prepared diamond-knife ultramicrotome sections of the shell, and examined these by transmission electron microscopy both before and after decalcification. The structure is summarized in text-fig. 3. The continuous sheets of interlamellar matrix are a distinctive feature of nacreous structure, not found in other molluscan shell structures. If nacre is decalcified, separate sheets of organic matrix are released; if the organic matter is destroyed with sodium hypochlorite solution, sheets of aragonite (probably still containing some intercrystalline and intracrystalline matrix) are liberated. Diagenesis or weathering frequently has the same effect, and fossil nacreous shells are often 'flaky'.

Nacre has a regular crystal orientation. the *c* axis of aragonite is always normal to the laminae. On the growing surface of the shell, especially when growth is slow, euhedral crystals of aragonite may be formed (Schmidt 1924, Wada 1961). Wada showed that the commonest forms developed in the zone normal to the *c* axis in the pearl oyster *Pinctada* are (110), usually predominant, and (010), and that the orthorhombic *b* axis of the crystals are aligned in parallel growth normal to the growing edge of the mantle. Grégoire (1962) found that in *Nautilus* (010) was dominant, so that the crystals were elongated along *a* and this axis was normal to the growth-lines.

The fine structure of the interlamellar matrix has been described by Grégoire (1957, etc.). It consists of reticulated sheets of protein, the pattern of the reticulations being characteristic of the class (Gastropoda, Bivalvia, Cephalopoda). In the Bivalvia the reticulations are fine and the structure correspondingly dense. Grandjean, Grégoire, and Lutts (1964) recorded preservation of this pattern in some fossils, but in others it is

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EXPLANATION OF PLATE 31

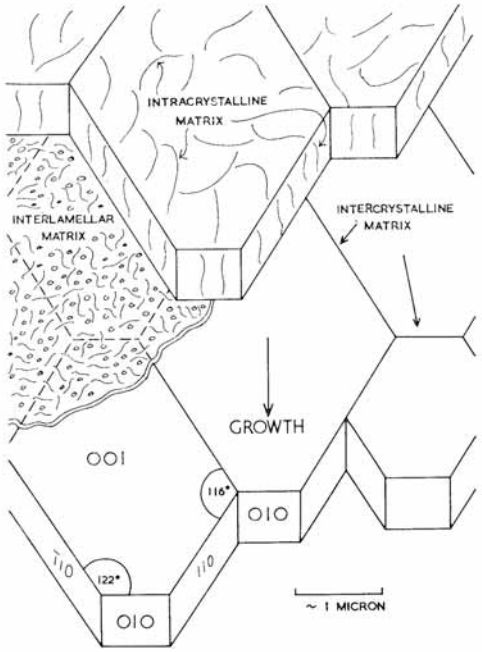
Plates 31–34 and figs. 2–4 of Plate 35 are electron micrographs of carbon replicas of broken or polished and etched sections of the shell of *Praemytilus strathairdensis*. Printed direct from film exposed in the microscope; shadows are white. Vertical sections are normal to the shell surface; horizontal sections parallel to it. Longitudinal sections are parallel, and transverse sections normal, approximately, to the axis of greatest growth of the shell.

Fig. 1. Nacreous structure. Broken vertical surface approximately normal to the laminae. Single-stage replica, ×6,800 (scale measures 10 μ).

Fig. 2. Nacreous structure. Polished and etched vertical section approximately normal to the laminae. Two-stage replica, ×7,100 (scale measures 10 μ).

diagenetically altered to a meshwork of irregular swellings, and this change could also be produced by heating a modern shell (Grégoire 1965).

Wada (1961) studied seasonal variations in the crystal size and structure of nacre on the growing surfaces of *Pinctada* shells. He showed that when nacre deposition was fastest, in the autumn, many rather small (about 4 μ) and uniform crystals were formed.



TEXT-FIG. 3. Generalized structure of bivalve nacre. Two laminae viewed obliquely in the *yz* plane of the constituent aragonite crystals, which are arranged in parallel growth. The laminae are separated by sheets of interlamellar matrix, of which a portion is shown with the reticulate structure drawn diagrammatically. Single crystals of aragonite are separated by intercrystalline matrix and contain intracrystalline matrix as thin sheets (shown diagrammatically in upper part of figure only). Growth in bivalves is in the direction of the *y* axis. The diagram shows structure only; it does not represent a stage in growth. (Based on the work of Wada, Watabe, and Grégoire.)

As growth slowed down before the winter cessation, crystals larger than 6 μ were formed together with very small ones of less than 2 μ. When growth started again in spring very small crystals predominated at first. Slow growth resulted in the best-formed aragonite crystals whereas fast-formed ones were rounded; during growth-halts resorption sometimes occurred resulting in corroded crystals (Wada 1961; especially table VIII, p. 758).

Structure of nacre in P. strathairdensis. The preservation of fossil nacre, including its sub-microscopic detail, has been recorded by several authors, especially Grégoire (1959) and Grandjean, Grégoire, and Lutts (1964). Similar excellent preservation has been studied in this species using the electron microscope.

Carbon replicas were used for electron microscopy. The surfaces replicated were of two kinds: (1) broken surfaces of nacre either parallel, approximately normal, or oblique to the lamination, (2) polished and etched surfaces, usually normal to the lamination and either longitudinal or transverse with respect to the shell. Various polishing techniques were used and either 1% HCl or saturated EDTA was used for etching, for times varying from 30 sec. to 3 min. Because of their lower organic content the etching times for fossil shells are less critical than with recent ones. From either broken or etched surfaces either single-stage or two-stage carbon replicas were prepared. For *single-stage replicas* carbon was evaporated *in vacuo* directly on to the prepared surface. The shell was then dissolved in very dilute HCl or dilute EDTA, and the carbon films floated free. They were transferred to distilled water before being picked up on grids for examination in the Philips 200 electron microscope. For *two-stage replicas* acetate peels were prepared of the chosen surfaces, by placing the surface on cellulose acetate with a few drops of acetone, allowing to dry, and stripping off. The peels were washed in HCl to remove adhering aragonite. The peels were then shadowed with carbon in the usual way. The area to be examined was cut out from the peels under a binocular microscope, the acetate dissolved in acetone and the carbon replicas floated off on distilled water before being picked up (from above) on parlodion-coated grids for electron microscopy. By making the cut-out areas of distinctive shape the orientation of these two-stage replicas with respect to the shell could usually be maintained. This is not possible, with the method employed, in the single-stage replicas, which also suffer from the fact that the method is destructive. However, single-stage replicas of broken surfaces are the simplest of possible replication techniques, and the most free from the danger of producing artefacts.

Vertical sections of *P. strathairdensis* nacre show the familiar brick-wall structure. In the inner layer the laminae are rather coarse (greater than 1 μ) and show the structure particularly clearly (Pl. 31, fig. 1, of a broken section; Pl. 31, fig. 2, of a polished and etched section). The vertical strips of intercrystalline matrix define the individual aragonite crystals, and it can be seen despite imperfect replication of the matrix strips that many of the crystals in Plate 31 are between 5 and 10 μ across. Plate 35, fig. 4, shows indications of a structure, presumably the network of intracrystalline matrix, within the individual aragonite crystals. Observations with the light microscope show that this coarse, regular nacre has the aragonite *c* axis normal to the laminae, as in modern nacre (Pl. 35, fig. 1).

The shells of *P. strathairdensis* break easily along certain planes parallel to the lamination. These surfaces were examined mostly by single-stage replication. Some of them (Pl. 32, fig. 1) proved to bear very well preserved, sharply euhedral crystals of aragonite, showing parallel growth and development of (101) and (110) faces. They are apparently identical to the crystals on modern nacre described and figured by Wada (1961, p. 757, figs. 102–4, etc.). Their orientation with respect to the growth direction of the shell is not known. Plate 32, fig. 2, shows small rounded objects up to 0·2 μ in diameter scattered over the surface of the larger crystals. These resemble the crystal seeds described by Watabe *et al.* (1958, p. 282, fig. 1) as the early stages of the formation of

EXPLANATION OF PLATE 32

For explanation of preparation of electron micrographs see Plate 31. The scale shown measures 10 μ.

Fig. 1. Nacreous structure. Horizontal broken surface parallel to laminae. Euhedral aragonite crystals. Single-stage replica, ×7,350.

Fig. 2. Preparation as fig. 1. Euhedral aragonite crystals and (?) crystal seeds. ×5,300.

calcite crystals in oysters. The diameter of the large crystals is about 12–14 μ in Plate 32, fig. 2, and 6–8 μ in Plate 32, fig. 1. Other broken surfaces showed smaller and less regular polygons. Sometimes these were aggregated into apparently continuous sheets, with the crystal boundaries (defined by intercrystalline matrix) not conforming to any regular crystal shape. In other cases the polygons, although irregular, remained distinct from each other and the gaps between them were presumably filled, in life, with organic matrix, or were void. The diameter of the irregular polygons varied from about 0·5–3 μ. An acetate peel of a broken surface showed, under the light microscope, fragmentary growth-spirals similar to those described by Wada (1961, p. 767).

The variations in *P. strathairdensis* may be related to the supposedly seasonal growth variations which are also reflected in the vertical thickness of laminae (see below). It has not been possible so far to relate the two types of variation accurately, though it does seem that the crystals in the thick regular nacreous laminae are often fairly large in diameter ($> 6\ \mu$).

When fragments of shell are decalcified they yield coherent but brittle sheets of brown-coloured organic matrix, representing part of the original interlamellar matrix. The chemical composition of this material is discussed below. Examined in the electron microscope by methods similar to those of Grégoire (1959) it has so far failed to show well-preserved ultrastructure of the kind figured by Grégoire from recent shells and some fossils. Instead it shows irregular swellings said to be characteristic of diagenetically altered fossil material (see Grandjean, Grégoire, and Lutts 1964, pl. II, etc.). More work is needed to see if all the *P. strathairdensis* material is similarly affected.

Vertical and horizontal sections examined by the replica techniques described above show 'sheets' corresponding positionally to the organic matrix. These may, in the case of two-stage replicas, be actual pseudo-replicas of the organic matrix itself, pulled off in making the peel (this certainly happens with recent shells), or they may be acetate which has penetrated cracks during the making of the peel. It is frequently impossible to tell the difference for certain (cf. Grégoire 1962, p. 8, footnote). On single-stage replicas folded-over carbon films can also be confused with true sheets of organic matrix, unless the matrix shows definite ultrastructure.

Thus *P. strathairdensis* nacre shows crystallographic features identical to those found in modern bivalve nacre, and some details of the relationship between the crystals and the organic matrix have been preserved. In the following paragraphs the distribution of nacre and other structures within the shell is described.

Periostracum. In thin sections of limestones, which consist largely of the aragonitic shells of *P. strathairdensis* cemented by calcite, the external surfaces of the shells are bordered by a thin sheath, about 5–15 μ thick, which is now composed of clear calcite devoid of internal structure. Usually the sheath adheres to the shell surface, but in places it has buckled and partially broken away from it. Such sheaths are only found on the external, never internal, surfaces of *Mytilus* shells, and have not been found on constituents of the limestones other than shells. Their spatial relations suggest that they are calcite-replaced periostraca. Presumably the conchiolin of the periostraca was replaced by calcite, while that of the calcareous layers was not, because it was external to the shell and not enclosed in aragonite. Also Hare (1963) shows that the amino-acid composition of the periostracum of *Mytilus californianus* differs from that of the protein matrix of the calcareous layers. Calcite has replaced a variety of minerals in these rocks,

and in the Ostracod Limestones a little higher in the succession the 'chitinous' carapaces of *Euestheria* have been replaced. No electron micrographs have been made, but similar sheaths on gastropods from the Reptile Bed of the Mytilus Shales (Hudson 1963, 1966) have been seen on micrographs. They showed no structures apart from calcite crystal boundaries.

Outer layer. This is fairly uniform in thickness over the major part of the shell. Typical values are: 80 μ at the pallial line in a small shell; 200 μ at the pallial line and 140 μ near the centre of a large shell; and several measurements of around 150 μ on apparently adult shells.

In thin sections with the light microscope the structure appears homogeneous, but on electron micrographs the structure is revealed as typically nacreous, with fine laminae. The thickness of these has been estimated by measuring groups of from 12–60 laminae and calculating the mean. Within such groups the individual lamina thickness is fairly uniform. The range of mean values for the main part of the shell is 0·32–0·51 μ, with a grand mean of 16 determinations (mostly of different parts of one shell) of 0·41 μ. This means that the outer layer, given a mean thickness of 140 μ, contains about 340 laminae in the central part of an adult shell. There is a tendency for lamina thickness to increase towards the ventral margin as the thickness of the outer layer increases. Beyond the pallial line, in the thickened reflexed margin, the distinction between inner and outer layers, in the absence of a myostracum, cannot be made on lamina thickness. In this region laminae have a mean thickness of about 0·7 μ.

Myostracal layers. Between the inner and outer shell layers, most sections show a layer about 3 μ thick (sometimes up to 10 μ), which is not divided into nacreous laminae. Its structure, where discernible, appears to be coarsely prismatic with the columns almost as wide as they are high. By analogy with modern mytilids (Schmidt 1924; Hudson, unpublished), this is interpreted as a myostracal layer. In the main part of the shell it must represent pallial myostracum or the myostracal layers associated with the posterior musculature. It is emplaced between the main shell layers, as the shell grows, because the pallial line is the border of the area of secretion of the inner layer. In this main part of the shell the myostracum is parallel, or nearly so, to the nacreous lamination (Pl. 33, fig. 1), but towards the margin it is oblique to, and truncates, the laminae of the outer layer (Pl. 35, figs. 2, 3).

Myostracal layers, which are similar in internal structure to the pallial myostracum, occur associated with the anterior adductor muscle and the pallial line immediately posterior to it, in the trough between the main part of the shell and the reflexed ventral margin. Some of these are enclosed entirely within the inner layer. The complex structures of this region are further described below.

EXPLANATION OF PLATE 33

For explanation of preparation of electron micrographs see Plate 31. The scale shown measures 10 μ.

Fig. 1. Myostracal layer in nacre; outer layer at top, inner layer beneath. Polished and etched vertical transverse section. Two-stage replica, × 7,000.

Fig. 2. Sub-layer junction in inner layer nacre. Later formed sub-layer is in lower left of photograph. Polished and etched vertical transverse section. Two-stage replica, × 7,000.

Inner layer. This reaches a thickness of at least 1·5 mm. in the post-umbonal region of thick adult shells, and extends to the pallial line where it forms a feather-edge. The microstructure is typically nacreous as seen by both light and electron microscopy. The most conspicuous feature is that the layer is divided into several sub-layers. As seen in vertical section, each sub-layer consists of clear, coarsely laminated nacre at its outermost (i.e. oldest) part, and for most of its thickness. The thickness of laminae decreases gradually, and at the junction with the next sub-layer there is a zone of fine laminae, not easily resolvable with the light microscope. Between crossed nicols, with the main part of the nacre in extinction, the junction zone shows up as speckles of light, apparently because the aragonite crystals are less well orientated there.

On electron micrographs, the layer junction appears as a group of from 5–20 (approx.) laminae which are much finer than the adjacent ones. They tend to grade into those above (i.e. older), and have a sharp junction with those below, but their limits may be difficult to define. Frequently the junction zone has acted as a weak zone in etching so that replication is poor. In the main part of the shell the laminae in adjacent sub-layers are parallel or nearly so (Pl. 33, fig. 2).

The maximum number of sub-layers seen in a shell is about eight, and this number or thereabouts is frequently attained. The range of thickness of sub-layers is not large (about 150–250 μ), and thick shells have more sub-layers than thin ones. This is consistent with their having been added throughout the life of the animal at a constant rate. Apparently similar sub-layers are found in the inner-layer nacre of the pearl oyster, *Pinctada*, where each sub-layer is interpreted as representing one year's growth (Wada 1961, p. 727, fig. 41).

Sub-layers and laminae. One transverse section of the post-umbonal region (E 203 D) provided particularly good replication of laminae for measurement by electron microscopy, and more detailed measurements were made on it. The number of laminae in each sub-layer was estimated and the results are summarized in text-fig. 4. It was not possible to count all the individual laminae across the sub-layers, because of interruption by grid bars and imperfect replication. Instead the thickness of each sub-layer was measured in the light microscope, and then electron micrographs were taken of each sub-layer junction and of typical nacre within each sub-layer. From these micrographs the number and thickness of laminae actually photographed could be determined, and mean thicknesses estimated for the remaining laminae. Thus the total number of laminae for each sub-layer was estimated. Obviously this method of calculation is not ideally precise. The range obtained was 120–230 laminae per sub-layer. The outer (first-formed) sub-layers have, in general, finer laminae than the inner ones (mean of 0·8–0·9 μ for the uniform central part of the outermost sub-layer, compared with 1·4–1·5 μ for several separate determinations on the inner four sub-layers). The fine laminae at sub-layer junctions have mean thicknesses around 0·5–0·7 μ. These measurements were all made on one carbon replica, but other parts of the same shell and of different shells gave similar results.

Structure of the reflexed margin. The same transverse vertical section (E 203 D) that was used to measure the laminae described in the last paragraph also gives a section through

the reflexed ventral margin, posterior to the anterior adductor muscle scar. This has been examined by means of peels and electron micrographs. Random sections of the same region, both approximately longitudinal and approximately transverse, have been studied in thin sections of limestones. The structure is complex and not fully understood. However, certain points can be established; in particular, the sharp division into two layers, characteristic of the main part of the shell, does not seem to hold.

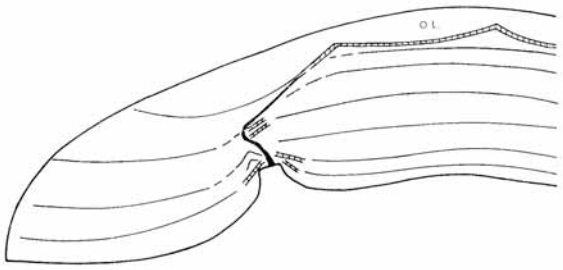
LAYER OR SUBLAYER	LAYER THICKNESS	MEAN LAMINA THICKNESS	ESTIMATED No. OF LAMINAE
OUTER LAYER	140	(0·41)	(340)
MYOSTRACUM	3	—	—
INNER LAYER: SUBLAYER 1	120	0·83 0·94 0·56	150
2	220	1·3 0·94 1·0 0·58	220
3	290	1·0 1·4 1·1 0·54	230
4	220	1·2 1·4 1·0 0·7	160
5	150	0·95 1·4 0·98 0·54	130
6	170	1·3 1·5 1·2 —	120
7	120	0·86 1·3	100(+?)

TEXT-FIG. 4. Data on laminae in a vertical section of *Praemytilus* nacre. Thicknesses are in microns. Figures in brackets extrapolated from different sections. The broken lines at the base of each sub-layer delimit the transition zone of thin laminae at sub-layer junctions. For explanation, see text.

Text-fig. 5 is based on the polished section and peels of E 203 D, incorporating some evidence from electron microscopy. Note that (1) the outer layer thickens towards the pallial line. (2) The outer sub-layers of the inner layer abut against the outer layer in this same region. (3) The myostracum separating the outer and inner layers disappears in the region of the pallial line. (4) At the pallial line the sub-layers of the inner layer are sharply curved into 'anticlines', some of which include prismatic layers identical to myostraca. Sharp angular breaks between sub-layers are present (Pl. 34). (5) Within the reflexed margin, beyond the final position of the pallial line, all laminae are more or less

parallel and there is no myostracum, so that there is no clear distinction between 'inner' and 'outer' layers. However, at least part of the thickness is probably 'inner' layer, because it includes sub-layers like those of the inner layer proper. Coloration in thin-section, and the thickening of the outer layer towards the pallial line which was mentioned above, suggest that the 'outer layer' is nevertheless rather thick, as drawn in the figure. Other, less precisely orientated, sections show similar relations.

The relationships described imply that when the first few sub-layers of the inner layer were deposited the reflexed margin consisted entirely of 'outer layer', so that the pallial



TEXT-FIG. 5. Structure of the reflexed margin in a vertical transverse section of *P. strathairdensis*. O.L., outer layer. Myostracal layers shown in brick pattern. Trend of laminae in inner layer shown by sub-layer boundaries. The black line above the pallial line represents a crack in the specimen. Structures generalized, especially in the zone of complex folds above the pallial line. For detail of part of this region, see Plate 34. Plate 35, fig. 1, corresponds approximately to the right-hand end of this figure. Drawn from an enlargement of an acetate peel. The shell is approximately 1·5 mm. thick.

line marked the junction between the layers, as in the main part of the shell. Subsequently, the margin was formed of material identical to the inner layer, so that the pallial myostraca and the unconformities of growth associated with the deeply impressed pallial line of the adult came to lie entirely within the inner layer.

If this is the case, the simple generalization that the outer layer is deposited by the mantle edge and the inner layer by the mantle surface within the pallial line, needs to be modified as regards this part of the shell. This is not surprising when the greatly different structural requirements of the two regions are considered. Probably the apparent cessation of shell-secreting activity by the mantle edge at the reflexed ventral margin is related to the fact that, after a certain point in ontogeny, the shell ceased to grow in the plane of the commissure in this region but only became thicker. For this, the type of mantle activity represented by the deposition of 'inner-layer' is sufficient, and the mantle edge no longer needs to extend itself or to produce new epithelial cells as it does in a normal marginal region. Plate 34 shows an example of the relationship between laminae, sub-layers, and myostracal layers in the region of the pallial line. The complex geometry and particularly the sharp truncations of earlier laminae may imply that some resorption of shell is necessary during the re-positioning of the pallial muscles which produces the successive layers of myostracal material.

MINERALOGY AND CHEMISTRY OF THE SHELLS

The excellent physical preservation of the microstructure suggested that a chemical investigation of the shell carbonate and organic matter might yield results of interest for comparison with modern shells. Results obtained so far are given here.

Mineralogy. The presence of aragonite in well-preserved *P. strathairdensis* shells was first conclusively shown by powder photographs taken by Dr. P. Gay at Cambridge (Hudson 1963). Later, a series of shells was selected to range from excellently preserved to porous and 'chalky', and analysed using the X-ray diffractometer procedure of Lowenstam (1954*a*) for calcite–aragonite ratio. All were aragonite, with calcite below the limit of detection (about 1%). This agrees with the results of Hallam and O'Hara (1961) that 'chalkification' does not necessarily involve a mineralogical change, and with unpublished results of the author's on other shells from the Jurassic and from the California Pleistocene terraces. Thin sections of limestones containing *P. strathairdensis* shells, cemented and infiltrated along cracks by sparry calcite, were tested using Feigl's solution, and the shells shown to consist of aragonite. Elsewhere, sometimes in the same rock, *Mytilus* shells have recrystallized to calcite (Hudson 1965).

Strontium–calcium ratios. Strontium analyses of *P. strathairdensis* shells were made by optical emission spectroscopy and by the electron microprobe. A series of four shells from very well preserved to porous and 'chalky', previously shown to be aragonite as described above, were analysed spectroscopically for Sr and Mg by the methods used for brachiopod shells by Lowenstam (1961). The results are given in Table 1; each number is the mean and standard deviation of mean from three separate determinations. The apparently anomalous result (E 217) was repeated and confirmed. The results from the best-preserved shells are consistent.

Two well-preserved specimens were used for exploratory analyses by electron microprobe. Vertical transverse sections were made of the region behind the umbo where the inner layer is thick, and these were polished and coated with carbon in the usual way. Step-scan analyses of 1 μ spots were made at 10 μ intervals across the shell, Sr $L\alpha$, Ca $K\alpha$, and Mg $K\alpha$ count-rates over 20 sec. being recorded simultaneously. The Ca figures were used to make sure that the spot being analysed was aragonite (not a crack, etc.); the Mg figures were too low for estimation. The Sr figures were compared by direct proportionality to a strontianite standard containing 55% Sr. The mean Sr percentages for the two shells based on about 100 points each were 0·48% and and 0·47% respectively. Clearly these figures need confirmation, using standards closer in composition to the unknown and with corrections for atomic number effect, etc., but the agreement between these first results and the emission spectroscopy results is gratifying. With the

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EXPLANATION OF PLATE 34

For explanation of preparation of electron micrographs see Plate 31. The scale shown measures 10 μ.

Vertical transverse section in the region above the pallial line, between the reflexed margin and the main part of the shell. Outer layer uppermost. Shows complex folds in nacreous laminae and irregular myostracal layers. Two-stage replica, ×3,700.

probe it will be possible to explore variations in Sr percentage between layers and sublayers but the present data are insufficient for this. If variations can be found, this should put limits on the amount of diagenetic alteration undergone by the shells, since it is unlikely that minor variations would survive extensive trace element migration.

Interpretations of the present data are necessarily limited. The Sr figures are higher than those for modern aragonitic bivalves, though lower than those of aragonite secreted by the lower invertebrates (Lowenstam 1964). It is not possible at this stage to do more than speculate on possible biochemical evolution towards lower Sr/Ca ratios

TABLE 1

Strontium contents of aragonitic Mytilid shells

Number	*Specimen*	*Sr Wt. %*	*Atoms Sr/1000 Ca*	*Method or Reference*
E 203	*P. strathairdensis*, well preserved	0·49±0·02	5·6	S
E 218–1A	,, ,,	0·49±0·02	5·6	2
E 218–1B	,, ,, (same shell)	0·42±0·04	4·8	2
E 217	,, slightly 'chalky'	0·73±0·05	8·4	S
E 210	,, very 'chalky'	0·49±0·03	5·6	S
E 220–1	,, well preserved	0·48	5·5	P
E 220–2	,, ,,	0·47	5·4	P
—	*Cuneolus tippana* (U. Cret.), Tennessee	—	3·1	(1)
—	,, ,, (U. Cret.), Maryland	—	3·5	(1)
—	*Septifer sp.* (Recent), Palau	—	2·2	(1)
—	*Mytilus californianus, M. edulis* (Recent), Calif. nacreous layer (negative temperature dependence of Sr)	—	1·5–2·5	(2)

S = optical emission spectroscopy, P = electron probe, (1) = Lowenstam (1964), (2) = Dodd (1965). See discussion in text.

in aragonite within the Mytilidae, like that postulated by Lowenstam for certain gastropods. It is tentatively considered that the Sr figures of around 0·48% Sr (Sr/1,000 Ca = 5·5) are original and not diagenetic, but this needs more rigorous proof (cf. Turekian and Armstrong 1961). A further complication is the probable lagoonal habitat of *P. strathairdensis* (see below), so that the possible effects of abnormal salinity and water chemistry would also have to be considered. Nevertheless the figures for modern and Cretaceous Mytilidae, given in Table 1 for comparison, are interesting and further work should enable their significance to be assessed.

Organic matrix. Physical preservation of some organic matrix but with diagenetically altered ultrastructure has been described above in connexion with the structure of nacre. The proportion and chemical composition of this organic matrix were determined with an F & M Model 180 CHN Analyser, modified to allow the analysis of the organic fraction in the presence of shell carbonate. The organic matter is oxidized by heating in the presence of a catalyst, and the combustion gases passed over Cu and CuO. Peaks due to C (as Co_2), H (as H_2O), and N (as N_2) are separated by gas chromatography. The results were obtained as part of a more extensive investigation (Hudson, in press). Comparisons with modern Mytilidae indicate that (1) the total amount of organic carbon in the shells (mean of five specimens = 0·15%) is reduced to about 10–20% of

the probable original value (nacre of recent *M. californianus* = 0·65%. *Choromytilus palliopunctatus* = 1·0%, *M. smargdensis* = 1·9%). (2) The organic carbon/organic nitrogen ratio in the fossils (mean of five specimens = 23) is much higher than in the modern *Mytilus* nacre (range of several determinations 2·8–3·7). This indicates preferential loss of nitrogen and at least partial degradation of the original proteins, perhaps to 'kerogen-like' material. (3) High hydrogen contents beyond the H probably directly combined with the organic carbon. These amount to nearly 0·2% by weight of hydrogen, thought to be present as free water firmly trapped in the structure. It is not removed by drying at 110°. This excess water is a general feature of recent and fossil nacre (Hudson, in press.)

These data suggest extensive post-depositional alteration of the organic matrix so that it is unlikely to reveal details of its original composition.

DISCUSSION

Differences (or similarities) in microstructure, mineralogy, and chemistry between the species under discussion and other recent and fossil shells must be assessed with the following questions in mind: Are the differences original or are they the result of diagenetic alteration? If original, are they the result of taxonomic differences reflecting evolutionary history, or do they follow from the ecological habitat of the particular shells studied? Clearly the questions are linked and cannot profitably be considered separately from one another. In the following paragraphs taxonomic and ecological aspects are stressed and the question of diagenesis is dealt with as it arises.

Taxonomy and evolution. Praemytilus strathairdensis is distinct from any other described Jurassic species and has been found at only one stratigraphical horizon in one small basin of deposition. It is, however, morphologically closer to modern mytiliform species than most, or perhaps any, of its contemporaries and may therefore be significant in the evolution of the Mytilidae.

Cox (1937, 1940) and Newell (1942) discuss the history of the Mytilidae. *Modiolus* appears to be a long-ranging genus from which the other Mytilidae, including mytiliform species (i.e. *Mytilus sensu lato*) have evolved, perhaps several times. The Jurassic genera *Praemytilus* and *Falcimytilus* appear to be the earliest mytiliform genera which are undoubted members of the Mytilidae (i.e. excluding the Upper Palaeozoic Myalinidae,

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EXPLANATION OF PLATE 35

The outer shell layer will be uppermost, as in Plates 31–34, if this plate is viewed from the side.

Fig. 1. Photomicrograph of vertical transverse section, crossed polarizers. Thin partially broken outer layer at top; rest is inner layer showing division into sub-layers. Thin section, ×50 (scale measures 1 mm.).

Figs. 2, 3. Two figures of same electron micrograph with slight overlap between figures allowing continuity to be visualized. Junction between inner and outer shell layers in a vertical transverse section, towards the shell margin. Myostracal layer is oblique to, and truncates, the nacreous laminae of the outer layer. Inner layer laminae approximately parallel to the myostracum, which is somewhat irregularly developed. Two-stage replica, ×3,000 (scale measures 10 μ).

Fig. 4. Part of the same preparation as Plate 31, fig. 1. Detail of nacreous laminae, showing structure within aragonite crystals. Single-stage replica, ×33,000 (scale measures 1 μ).

and such Triassic and Jurassic genera as *Lycettia* which Cox (1937) considers may be descended from them, or whose internal structure is unknown). In harmony with this, the shell structure of *P. strathairdensis* is closely similar to that of modern tropical representatives of *Mytilus sensu lato* (see below) whereas its edentulous hinge agrees with that of *Modiolus*. The shell structure of *Falcimytilus* is unknown, unless the 'Upper Jurassic *M. mirabilis*' described briefly by Bøggild (1930, p. 273) is the same species as the Liassic *M. mirabilis* (Lepsius) which Cox (1940) suggested was a *Falcimytilus*. Bøggild's description, inferred from a poorly preserved specimen, suggests a shell structure further removed from modern *Mytilus* than that of *Praemytilus*, and closer to that of some modern *Modiolus* (an unnamed species described by Bøggild 1930, p. 273; and *Volsella capax* listed by Oberling 1964, p. 37).

The modern genus *Mytilus sensu lato* (i.e. smooth Mytilidae with terminal umbones in the adult and a hinge bearing teeth) was split into two subgenera by Jukes-Brown (1906) and into at least five genera by Soot-Ryen (1955), who did not regard his genera as necessarily closely related to one another. Whether any or all of these are direct descendants of *Praemytilus*, or whether they are later offshoots from, presumably, *Modiolus*, is pure speculation at this stage owing to lack of knowledge of the intervening history of the family. In either case it would appear that edentulous forms preceded those with teeth, which is not what would be expected from a recapitulation of ontogeny.

Palaeoecology. The palaeoecology of the Mytilus Shales as deduced from lithology and from a comparison of the fauna with modern representatives of the same genera has been described by Hudson (1963, 1966). *P. strathairdensis* is the dominant member of the fauna in the main part of the succession. It was concluded that the habitat of the species was a mud or silt bottom, where it probably attached itself by its byssus to shell or 'seaweed', in lagoons whose salinity no doubt fluctuated but was normally below that of the open sea.

The present results can perhaps add to this. The wholly aragonitic mineralogy and concomitant nacreous structure in both main layers agree with modern tropical and subtropical species of *Mytilus sensu lato* (Lowenstam 1954*a*, *b*; Hudson unpublished data). *M.* (*Perna*) *perna* from Brazil is wholly aragonitic in a temperature range of 18·9–27·8° C with a mean of 23° C. Temperate species of *Mytilus*, on the other hand, have a calcitic outer layer, and show an aragonite/calcite ratio which increases approximately linearly with temperature to the limit of their range at a mean temperature of about 20° C (Lowenstam 1954*a*). The Upper Cretaceous Mytilid *Cuneolus tippana* from the Coon Creek Formation of Tennessee is wholly aragonitic and wholly nacreous (Bøggild 1930; Lowenstam 1954*a*); it gave an isotopic palaeotemperature of 23° C whereas the range of palaeotemperatures of other members of the Coon Creek fauna was closely similar to the modern temperature range of *M.* (*P.*) *perna* quoted above (Lowenstam and Epstein 1954). This suggests a similar temperature response in Cretaceous Mytilidae as in modern ones, and extension to the Jurassic would predict high temperatures for the aragonitic *P. strathairdensis*. There is, however, a pronounced species effect in modern Mytilidae as shown, for instance, in the much higher aragonite percentages in temperate species of *Modiolus* ('*Volsella*') compared to *Mytilus* from the same temperature range (Lowenstam 1954*a*). The fact that *P. strathairdensis* probably lived in brackish water may also be relevant, since Lowenstam (1954*a*) and Dodd (1964) concluded that

reduced salinity probably favours increased aragonite percentage in *M. edulis*, though this has subsequently been disputed (Eisma 1966, Dodd 1966). Despite these complications, the fact that *wholly* aragonitic *Mytilus* and *Modiolus* are exclusively tropical to subtropical today is probably significant for the life-temperature of *P. strathairdensis*.

It has been shown above that the inner layer of *P. strathairdensis* shows sub-layers which are very similar to those interpreted as annual growth-layers in the nacre of modern pearl oysters by Wada (1961). This suggests seasonal growth. The pearl oysters stop depositing shell when the temperature falls below 13° C. In their isotopic study of the Bermuda fauna Epstein and Lowenstam (1953) concluded that many bivalves showed such a temperature threshold; in *Chama macerophylla* it was as high as 21° C. These results were not related to visible structures in the shell, however. The evidence for seasonal growth in *P. strathairdensis* may thus imply seasonal temperature fluctuations in the environment. The belemnite analysed in detail by Urey *et al.* (1951) came from the Upper Jurassic of Skye. It showed a mean temperature of 20·8° C (corrected to the new palaeotemperature scale) and an annual temperature-range of 6° C. Whereas the temperature need not have been similar in the Middle Jurassic, it is likely that the implied tendency to fairly marked seasonal temperature variations would already have been established in the same area.

The regular aragonite-organic matrix lamination in nacre suggests some small-scale rhythmic control which might be external. There is, however, no evidence at present on this. It does not appear to be a circadian rhythm. Wada's (1961) data on pearl oysters give (by calculation) over 500 laminae per growth season. The number per supposed season in *P. strathairdensis* is less than 250.

Many of the doubts expressed about quantitative conclusions from the data presented come from uncertainty about the salinity régime of the Great Estuarine Series lagoons. It is hoped (1) to obtain isotopic palaeotemperatures and trace-element data for fully marine faunas of the same general horizon and region, (2) to obtain carbon and oxygen isotopic data on apparently unaltered shells from the Great Estuarine Series and try to relate these to palaeosalinities. Combined chemical and structural studies, preferably on several members of the same fauna, may enable much more precise interpretations of temperature, seasonality, etc., to be drawn, as well as contributing data to evolutionary palaeontology.

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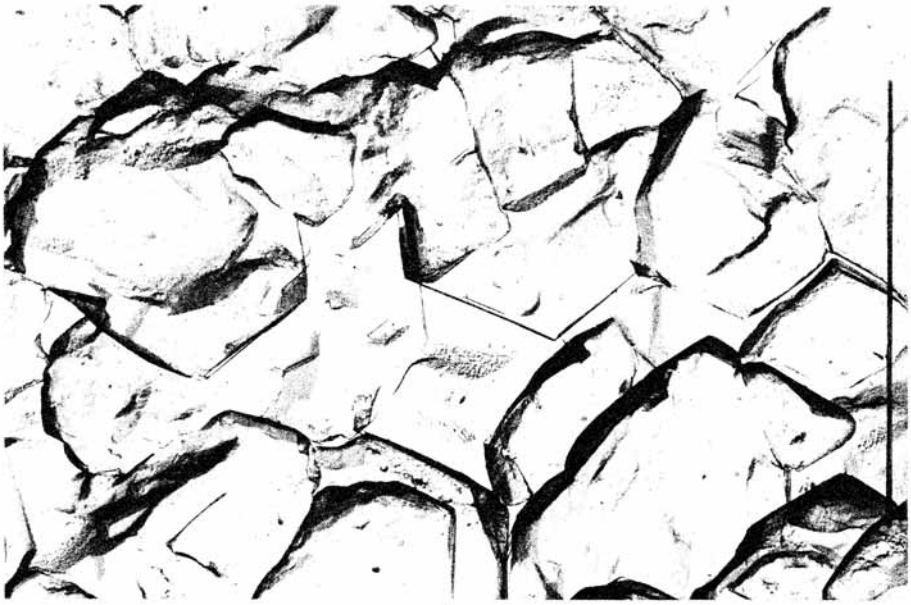

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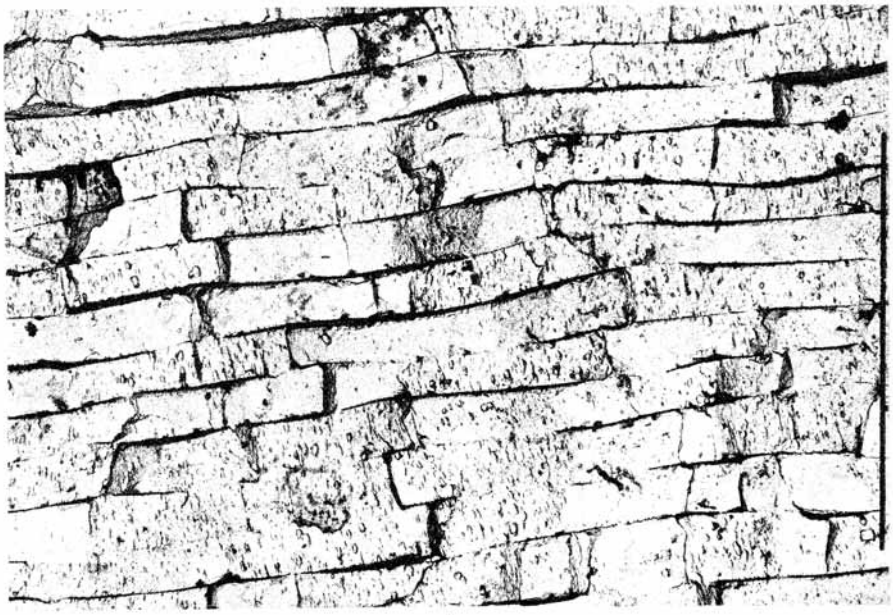
HUDSON, Jurassic mytilid shell microstructure



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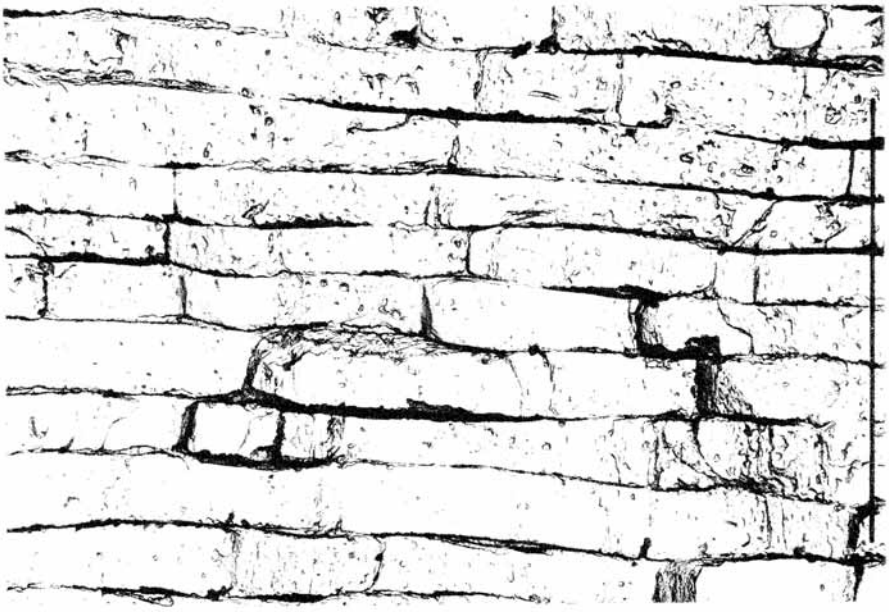

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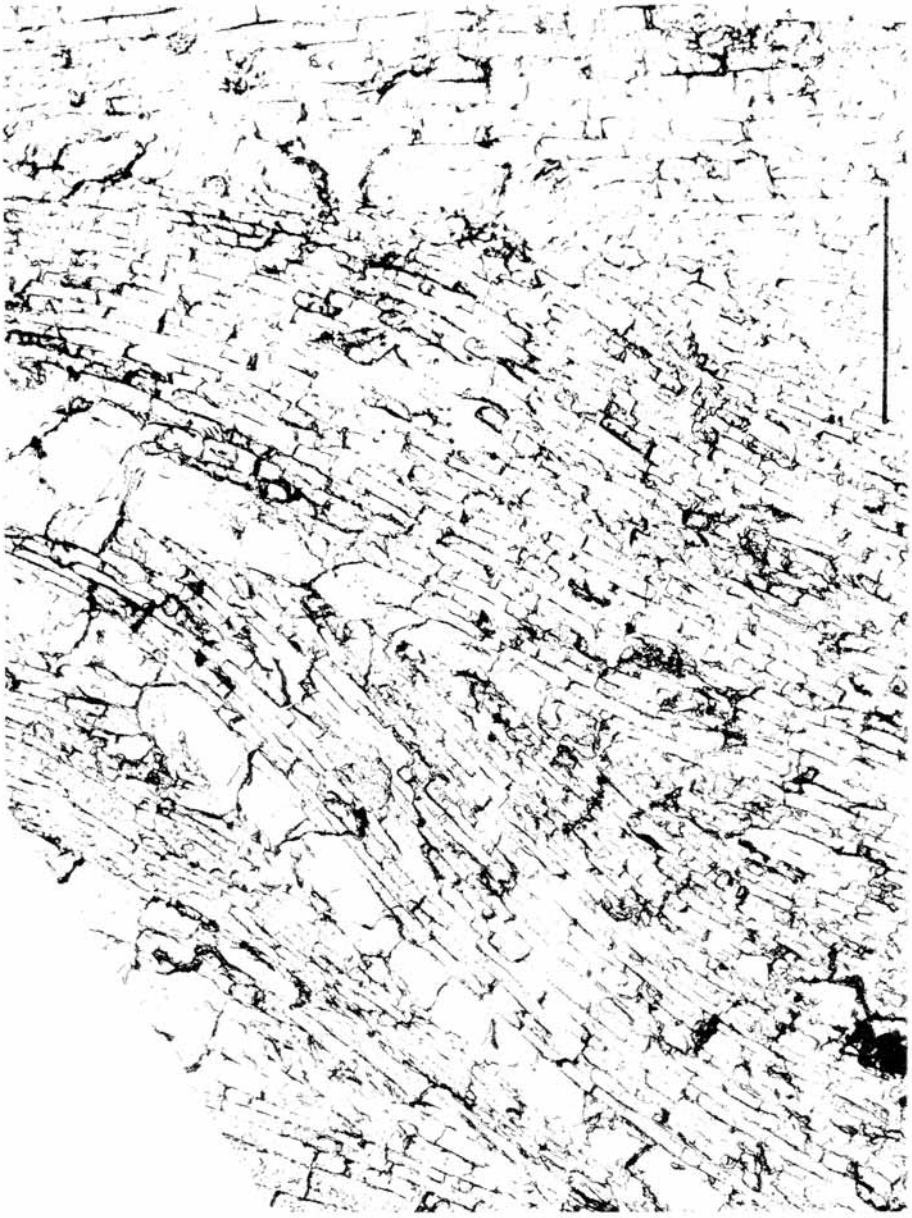

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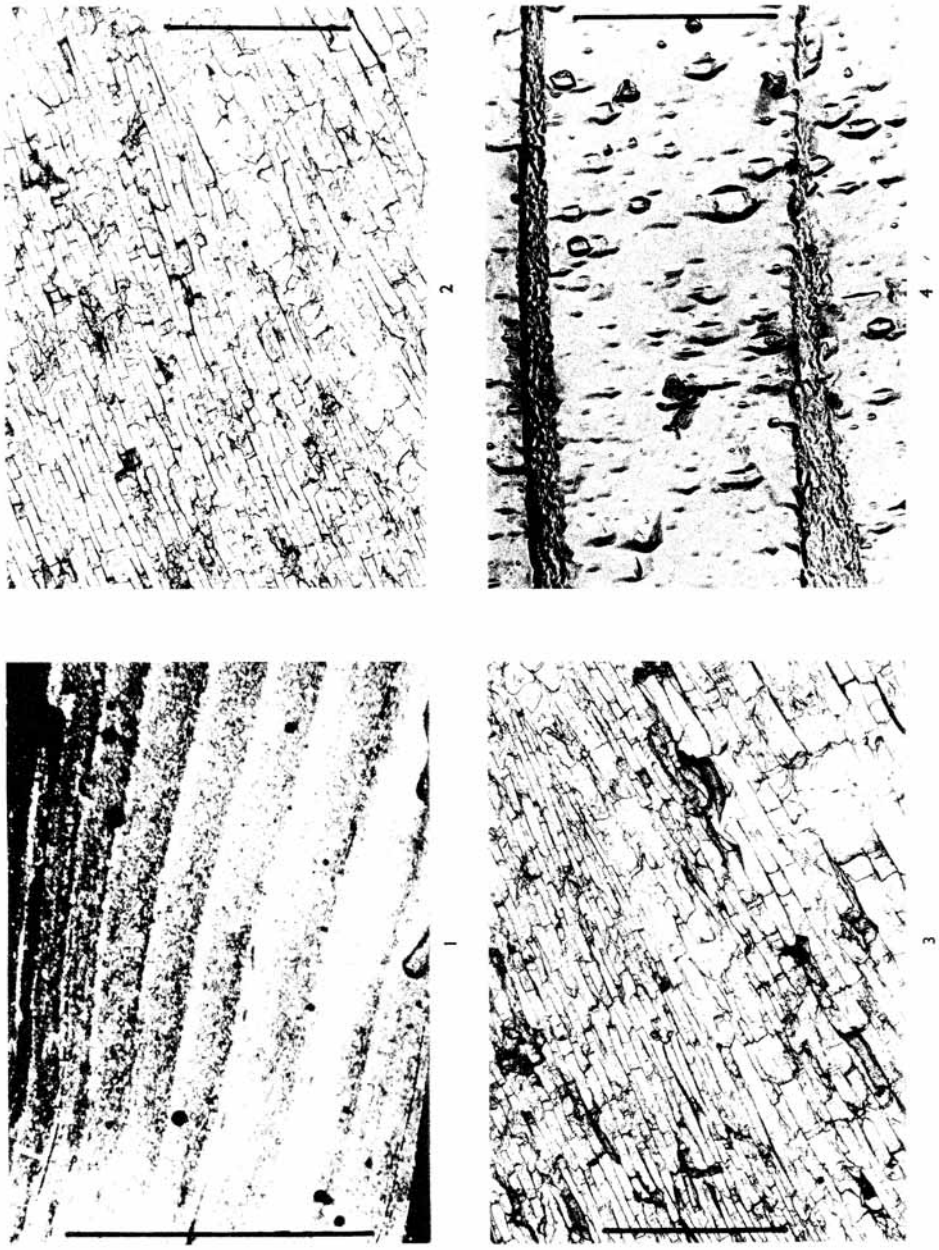

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